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DESCRIPTION OF A NEW LEPIDOPTERAN STRUCTURE, THE ABDOMINAL TUBERCLES

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ABSTRACT. Adult moths of the superfamily Cossoidea (Lepidoptera) have been found to possess paired tuberculate evaginations on abdominal tergites 2-8. At least in Cossidae, the tubercles appear glandular based on light and scanning electron microscopy studies. Similar "abdominal tubercles" have also been found in the lepidopteran families Andesianidae, Acrolophidae, Arrhenophanidae, Brachodidae, Carposinidae, and Pyralidae. The tubercles in these other families appear non-homologous to those in Cossoidea, suggesting that these structures have arisen multiply in independent lineages. Paired tuberculate invaginations also were found on the anterior margins of abdominal tergites 2-8 on adults of Megalopygidae, but these structures appear to be non-homologous with the evaginated abdominal tubercles of the Cossoidea.

Additional key words: abdominal glands, Cossidae, Cossulinae, Cossoidea

INTRODUCTION

In the course of a revision of the cossid moth subfamily Cossulinae (in preparation), adult moths throughout the superfamily Cossoidea (Cossidae + Dudgeoneidae) were found to possess paired tuberculate evaginations on abdominal tergites 2–8 (Fig. 1). These organs apparently have not been observed previously in any insect, including Lepidoptera. Although tuberculate structures similar to those described here have been described in the Tineoidea and Copromorphoidea by Kyrki (1983) as wart-like protuberances, these structures only occur on the 2nd abdominal sternite. The purpose of the present study was to fully characterize the structure of the "abdominal tubercles" in Cossidae, where they appear to be glandular, and to explore their presence/absence across other lepidopteran superfamilies to understand their possible phylogenetic significance.

MATERIALS AND METHODS

Taxon sampling (Table 1)

Representatives of all subfamilies within Cossidae, including nearly all species of Cossulinae, were examined by light microscopy for the presence of abdominal tubercles, as were the dudgeoneid genera *Acritocera* and *Dudgeonea*. One species, *Cossula arpi* Schaus, was selected for additional study using the SEM. Light microscopy was used to examine taxa broadly sampled across the Lepidoptera. The taxa examined apart from Cossulinae (64 species representing 49 families and 26 superfamilies) are listed in Table 1, showing their positions in the current best estimate of higher phylogeny (Kristensen and Skalski 1999). In Cossulinae, all known species were examined except '*Cossula*' *abnoba* Schaus, '*Cossula*' *alboperlata* Bryk, '*Cossula*' *magna* Schaus, '*Cossula*' *manes* Druce, '*Cossula*' *ophthalmodes* Hering, and '*Cossula*' *tacita* Druce, for which no material was available. The Cossoidea currently are hypothesized to be sister group to the Sesioidea, and these in turn to be most closely related to Zygaenoidea. Multiple families of both Sesioidea and Zygaenoidea were sampled. This clade in turn falls among the unresolved basal (non-obtectomeran) groups of Apoditrysia (Kristensen and Skalski 1999), for which the four other largest superfamilies were sampled. Additional groups examined included six non-ditrysian superfamilies, all four superfamilies of non-apoditrysian Ditrysia, and nine obtectomeran superfamilies including five superfamilies and nine families of Macrolepidoptera.

Specimen preparation

Specimens from taxa outside Cossulinae were examined using slide preparations in the National Museum of Natural History, Washington, D.C., and from the Australian National Insect Collection (ANIC) at CSIRO, Canberra, Australia (slide numbers in Table 1). For Cossulinae, abdomens were dissected by placing them in 10% KOH solution for approximately 12 hours at room temperature (72 degrees F) or for approximately 10 minutes when heated on a hot plate. The abdomen then was placed in 50% EtOH/water solution and the scales removed gently from the cuticle with a fine-tipped camel hair brush. The abdomen was cut along the spiracles with dissecting scissors in order to make both the ventral and dorsal sides visible when slide-mounted. Chlorazol black stain was used for approximately 15 minutes or until sufficiently stained a light blue. After staining the abdomen was placed in 95% EtOH for 10 minutes to remove any remaining water, transferred to clove oil for 10 minutes for further clearing, and then to xylene for 10 minutes to fix the cuticle The structures were then slide-mounted in Canada balsam.

Digital photography of the tubercles was

accomplished using slide-mounted structures and Auto-Montage (Synoptics Ltd.) software, which blends multiple images taken at various focal lengths to give one completely focused image. Scanning electron microscope images were taken using an Amray 1810 with a LaB6 (lanthanum hexaboride) source.

Results

Description of Tubercles

In the Cossidae, the tubercles occur in both sexes but are slightly less developed in females. The tubercles increase in size caudally (Fig. 1), with the first pair reduced to a small pore leading to an apparent internal gland (Figs 2, 8), and the caudal-most pair suberect and digitiform (Fig. 9). The anterior-most tubercles are minute, the more caudal pairs range up to approximately 0.1 mm in length (Figs 3–5), clearly visible under a dissecting microscope. In the representative of Cossulinae examined by SEM, an asymmetrical flap of tissue, possessing a fimbriate tip, extends from the apex of the tubercle (Figs 6–7).

It appeared initially that these organs were present only in Cossidae, because tubercles of similar size were seen in no other superfamily. However, upon closer inspection of the dudgeoneid genera *Acritocera* (Fig. 11) and *Dudgeonea* (Fig. 12), the tubercles were found,

Table 1. Lepidopteran taxa outside Cossulinae examined for the presence of abdominal tubercles. Family and superfamily nomenclature follows Kristensen and Skalski (1999) Slide numbers refer to specimens deposited at the National Museum of Natural History, Washington, D.C., and the Australian National Insect Collection (ANIC) at CSIRO, Canberra, Australia.

Superfamily	Family	Species (USNM/ANIC slide #)	Abdominal Tubercles present?
Non–Ditrysian superfamilies (6 of 13 sampled)			
Micropterigoidea	Micropterigidae	*Paramartyria immaculatella* Issiki (16454, 16453)	–
		Sabatinca aurella (Hudson) (91789, 16086)	–
Eriocranioidea	Eriocraniidae	*Eriocraniella mediabulla* Davis (3241)	–
Nepticuloidea	Nepticulidae	*Ectoedemia heinrichi* Busck (16848)	–
Incurvarioidea	Incurvariidae	*Tegeticula yuccasella* (Riley) (97859, 97820)	–
Palaephatoidea	Palaephatidae	*Palaephatus pallidus* Davis (21321, 21320)	–
Andesianoidea	Andesianidae	*Andesiana lamellata* Gentili (32428, 31763)	X
		Andesiana similis Gentili (32429)	X
Ditrysia - Nonapoditrysian superfamilies (4 of 5 sampled)			
Tineoidea	Acrolophidae	*Acrolophus popeanellus* (Clemens) (18177)	X
	Arrhenophanidae	*Arrhenophanes perspicilla* (Stoll) (23624, 23626)	X
	Psychidae	*Cryptothelea watsoni* Jones (69834)	–
	Tineidae	*Nemapogon* sp. (91883)	–
Gracillarioidea	Bucculatricidae	*Bucculatrix simulans* Braun (91984)	–
	Gracillariidae	*Caloptilia juglandiella* (Chambers) (92007)	–
		Caloptilia reticulata (Braun) (92010)	–
Yponomeutoidea	Acrolepiidae	*Acrolepiopsis incertella* (Chambers) (91672, 91666)	–
	Glyphipterigidae	*Glyphipterix bifasciata* Walsingham (77163, 77166)	–
	Ochsenheimeriidae	*Ochsenheimeria vacculella* Fischer von Röslerstamm (16126, 16138)	–
	Plutellidae	*Protosynaema eratopis* Meyrick (77666)	–
	Yponomeutidae	*Atteva punctella* (Cramer) (76651, 76661)	–
Gelechioidea	Blastobasidae	*Holocera gigantella* Chambers: slide DA 1835 (UCB)	–
		Holocera chalcofrontella Clemens (80995)	–
	Gelechiidae	*Gelechia turpella* (Denis & Schiffermüller, 1775) (6869, 6848)	–
		Gelechia versutella Zeller (86693)	–
	Glyphidoceridae	*Glyphidocera hulberti* Adamski (81243)	–
	Xyloryctidae	*Cryptophasa rubescens* Lewin (12544, 12543)	–

(continued)

TABLE 1. (continued)

Superfamily	Family	Species (USNM/ANIC slide #)	Abdominal Tubercles present?
APODYTRISIA - NON-OBTECTOMERAN SUPERFAMILIES (7 of 11 sampled)			
Zygaenoidea	Dalceridae	*Dalcera abrasa* Herrich-Schaeffer (28095, 28094)	–
		Dalcerina tijucana (Schaus) (28083, 28082)	–
	Limacodidae	*Acharia helenans* Dyar (slide numbers absent)	–
	Megalopygidae	*Megalopyge defoliata* Walker (28095)	–
	Zygaenidae	*Illiberis sinensis* Walker (12142, 12140)	–
Cossoidea	Cossidae	*Archaeoses polygrapha* (Lower) (H 28)	X
		Charmoses dumigani Turner (PG 907)	X
		Cossodes lyonetii White (96148)	X
		Idioses littleri Turner (PG 909, PG 910)	X
		Ptilomacra senex Walker (96149)	X
	Dudgeoneidae	*Acritocera negligens* Butler (ANIC 1550)	X
		Dudgeonea sp. (ANIC 2550)	X
Sesioidea	Brachodidae	*Brachodes appendiculatus* (Esper) (77547, 77548)	X
		Brachodes canonitis Meyrick (77592)	X
	Castniidae	*Telchin licus* (Drury) (96147)	–
	Sesiidae	*Alcathoe autumnalis* Engelhardt (75719)	–
		Paranthrene simulans (Grote) (75792, 75791)	–
Choreutoidea	Choreutidae	*Prochoreutis inflatella* (Clemens) (77118, 77119)	–
Tortricoidea	Tortricidae	*Phricanthes asperana* Meyrick (89912)	–
Alucitoidea	Alucitidae	*Alucita* sp. (63644)	–
Pterophoroidea	Pterophoridae	*Paraplatyptilia shastae* (Walsingham) (63247, 63248)	–
OBTECTOMERA - NON-MACROLEPIDOPTERAN SUPERFAMILIES (4 of 6 sampled)			
Copromorphoidea	Carposinidae	*Carposina nipponensis ottawana* Kearfott (22325)	X
	Copromorphidae	*Lotisma trigonana* (Walsingham) (77115, 77069)	–
Hyblaeoidea	Hyblaeidae	*Hyblaea puera* (Cramer) (107522, 110219)	–
Pyraloidea	Crambidae	*Maracayia chlorisalis* (Walker) (104689, 104684)	–
	Pyralidae	*Condylolomia participalis* Grote (106364, 104464, 104465)	X
Thyridoidea	Thyrididae	*Meskea dyspteraria* Grote (107524, 107528)	–
MACROLEPIDOPTERAN SUPERFAMILIES (5 of 11 sampled)			
Bombycoidea	Sphingidae	*Eumorpha achemon* (Drury) (3723)	–
Lasiocampoidea	Lasiocampidae	*Tolype velleda* (Stoll) (40969)	–
		Tolype minta Dyar (40967)	–
Drepanoidea	Drepanidae	*Drepana arcuata* (Walker) (56418, 56420)	–
Geometroidea	Geometridae	*Prochoerodes forcicaria* (Guenée) (56692, 56693)	–
	Uraniidae	*Psamathia placidaria* (Walker) (57164, 57165)	–
Noctuoidea	Arctiidae	*Halysidota ata* Watson & Goodger (57065, 38264, 38265)	–
	Lymantriidae	*Orgyia vetusta* Boisduval (52411, 52410, 52407)	–
	Noctuidae	*Cissusa valens* (Edwards) (40504, 40505)	–
		Papaipema furcata (Smith) (39418)	–
	Notodontidae	*Macrurocampa dorothea* Dyar (2765, 2714)	–

but they are much smaller than in most Cossidae. Some genera considered to be among the most primitive cossids (E. D. Edwards, pers. comm.) also were found to have small tubercles like those in *Dudgeonea* and *Acritocera*, including *Archaeoses* (Fig. 13), *Idioses*, and *Charmoses*, whose subfamily affinities are currently in doubt (Edwards 1996). The tubercles in Dudgeoneidae are approximately 0.01 mm in length and can be only seen with a compound microscope. Although similar in form to the tubercles in Cossidae, including the presence of a terminal pore, they are relatively uniform in size among abdominal segments.

In addition to Cossoidea, abdominal tubercles were observed (Table 1) in all representatives examined from Andesianidae (Figs 14–15), Acrolophidae (Figs 16–17), Arrhenophanidae (Figs 18–21), Brachodidae (Figs 22–23), Carposinidae (Fig. 24), and Pyralidae (Figs 25–26). These tubercles are similar in size to those in Dudgeoneidae, but differ in apparently lacking the terminal pore seen in Cossoidea.

Examination of the megalopygid species *Megalopyge defoliata* revealed paired tuberculate invaginations (as opposed to the evaginate tubercles described above) on the anterior margin of each abdominal sclerite (Figs 27–30). These invaginations are approximately 0.1 mm long and lack an apical pore. Occasionally one member of the pair can be missing from a given segment.

DISCUSSION

The function of the abdominal tubercles is unknown, but several observations suggest that, at least in Cossidae, they may be glandular. First, the tubercles in cossids possess an internal canal which opens to the outside through a terminal pore. Second, at the base of the tubercle (e.g. Fig. 9) there appears to be an enclosed chamber, plausibly interpreted as a gland. Third, the fimbriate tip of the tubercle seen under SEM is suggestive of an evaporative surface. Because the tubercles in Cossidae are so small, and occur in both sexes, it is unlikely that they are associated with long-range pheromone production. It seems more plausible that they could be involved in production of a close range pheromone, or a defensive chemical (Hallberg and Poppy 2003). Clearly, histological, physiological, and behavioral studies will be required to test these hypotheses.

From their distribution across major lepidopteran lineages (Table 1), it appears that abdominal tubercles have arisen sporadically in multiple, independent groups. With the possible exception of Brachodidae (see below), it seems unlikely that the tubercles in Cossoidea represent shared ancestry with any occurrences outside that superfamily. Lack of a terminal pore in tubercles outside Cossoidea further suggests non-homology of these. The paired invaginations found in Megalopygidae seem especially unlikely to be homologous to the other tubercles observed, which are never invaginations, but are rather evaginations from the abdomen.

While sampling outside Cossoidea was very sparse, these preliminary observations suggest that presence of abdominal tubercles might prove to be a phylogenetically informative character within several families and/or superfamilies when sampling is expanded. For example, tubercles were found in some but not all of the families examined within Tineoidea, and within Copromorphoidea and Pyraloidea as well.

If we accept the monophyly of Cossoidea (Edwards et al. 1999), it follows that the shared possession of tubercles is inherited from the ancestor of Cossidae and Dudgeoneidae. However, it is unclear whether this trait is a synapomorphy for Cossoidea. Recent evidence suggests that the sister group to Cossoidea is Sesioidea, within which the family relationships appear to be (Brachodidae (Sesiidae,Castniidae)) (Edwards et al. 1999). In Sesioidea, tubercles appear to occur only in Brachodidae. It is possible that this is an independent origin from that in Cossoidea. However, assuming that further sampling confirms that tubercles belong to the groundplan of Brachodidae, it would be equally parsimonious to assert that the tubercles arose in the common ancestor of the two superfamilies, and were subsequently lost in the sesiid/castniid lineage. There is no obvious way to distinguish these alternatives.

Within Cossoidea, variation in the development of the abdominal tubercles may provide a synapomorphy for a majority of Cossidae. As noted earlier, small and uniform-sized tubercles, the condition in Dudgeoneidae, are also found in several Australian genera thought to be primitive within Cossidae (E. D. Edwards, pers. comm.). Thus, the enlargement of the tubercles on the caudal abdominal segments in most genera of Cossidae may be a derived condition. Further study of cossid phylogeny is needed to test this hypothesis.

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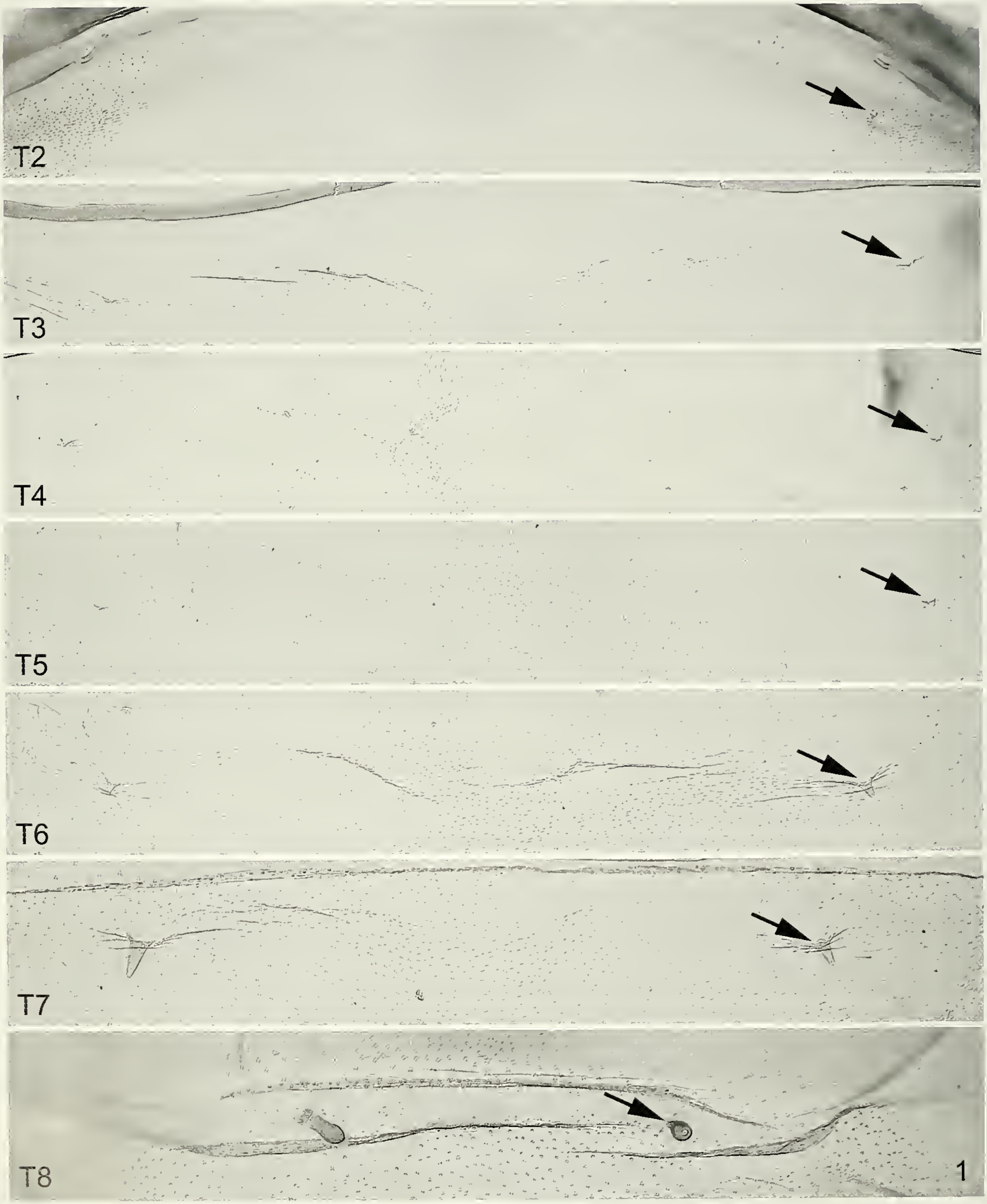
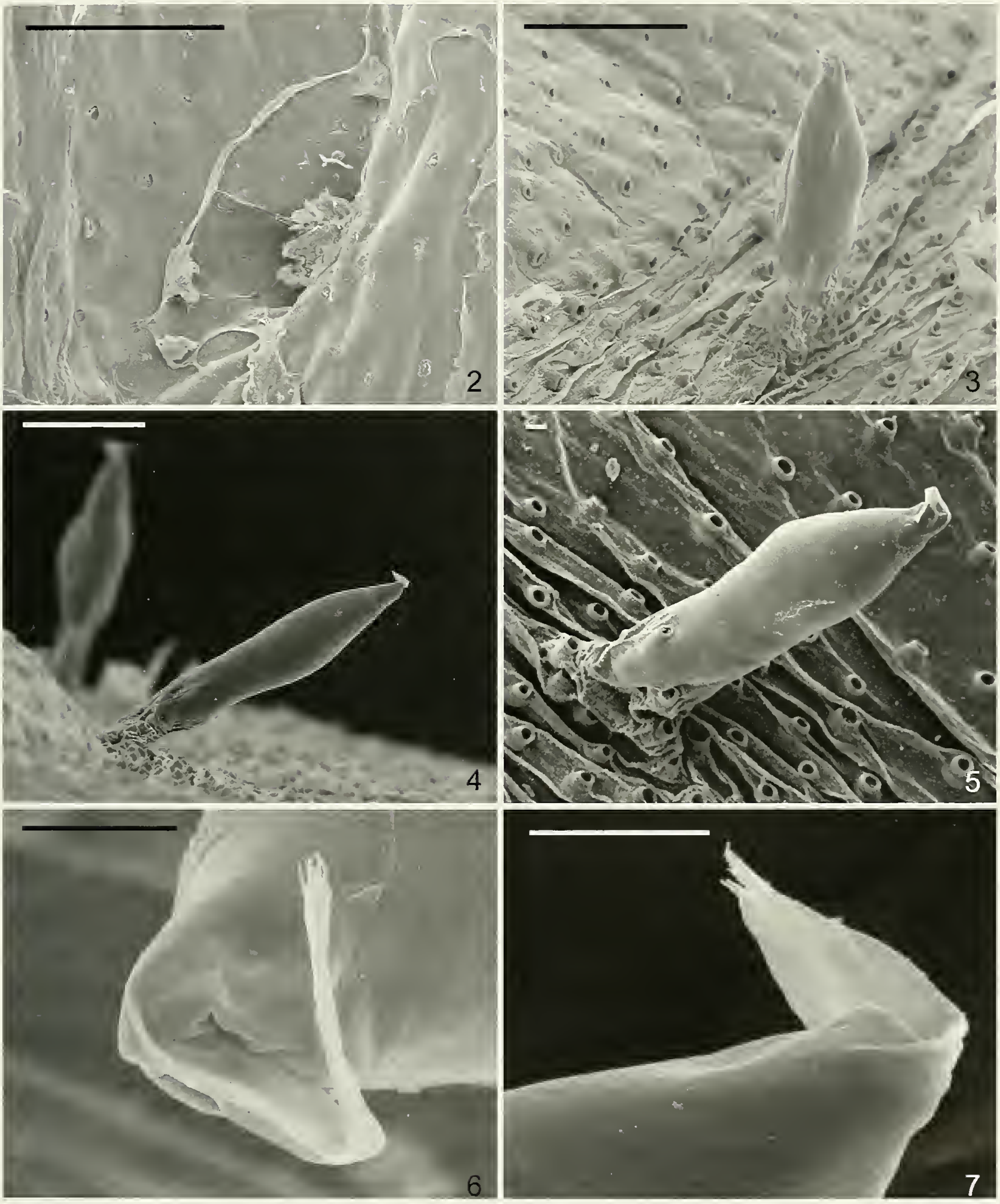
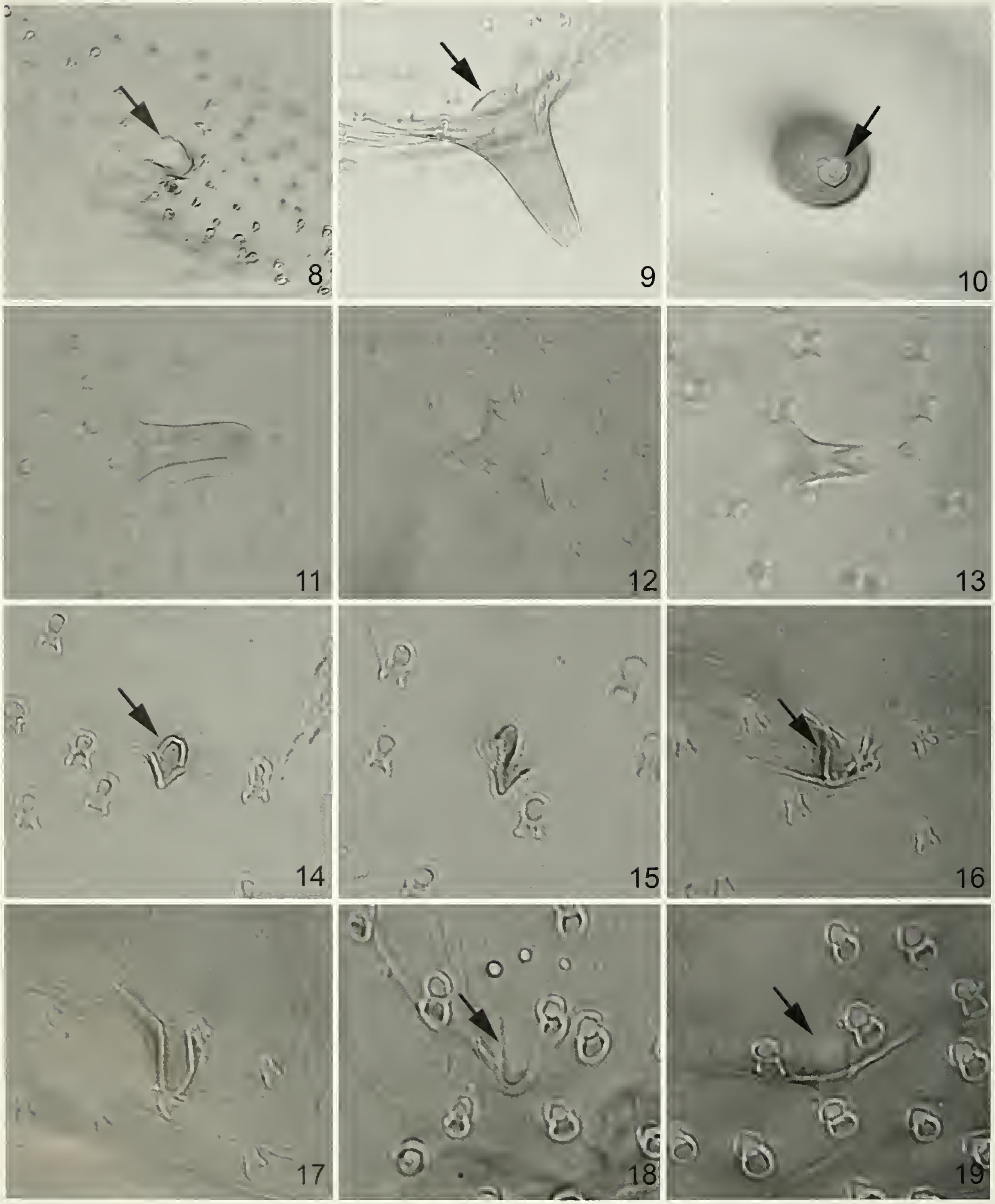


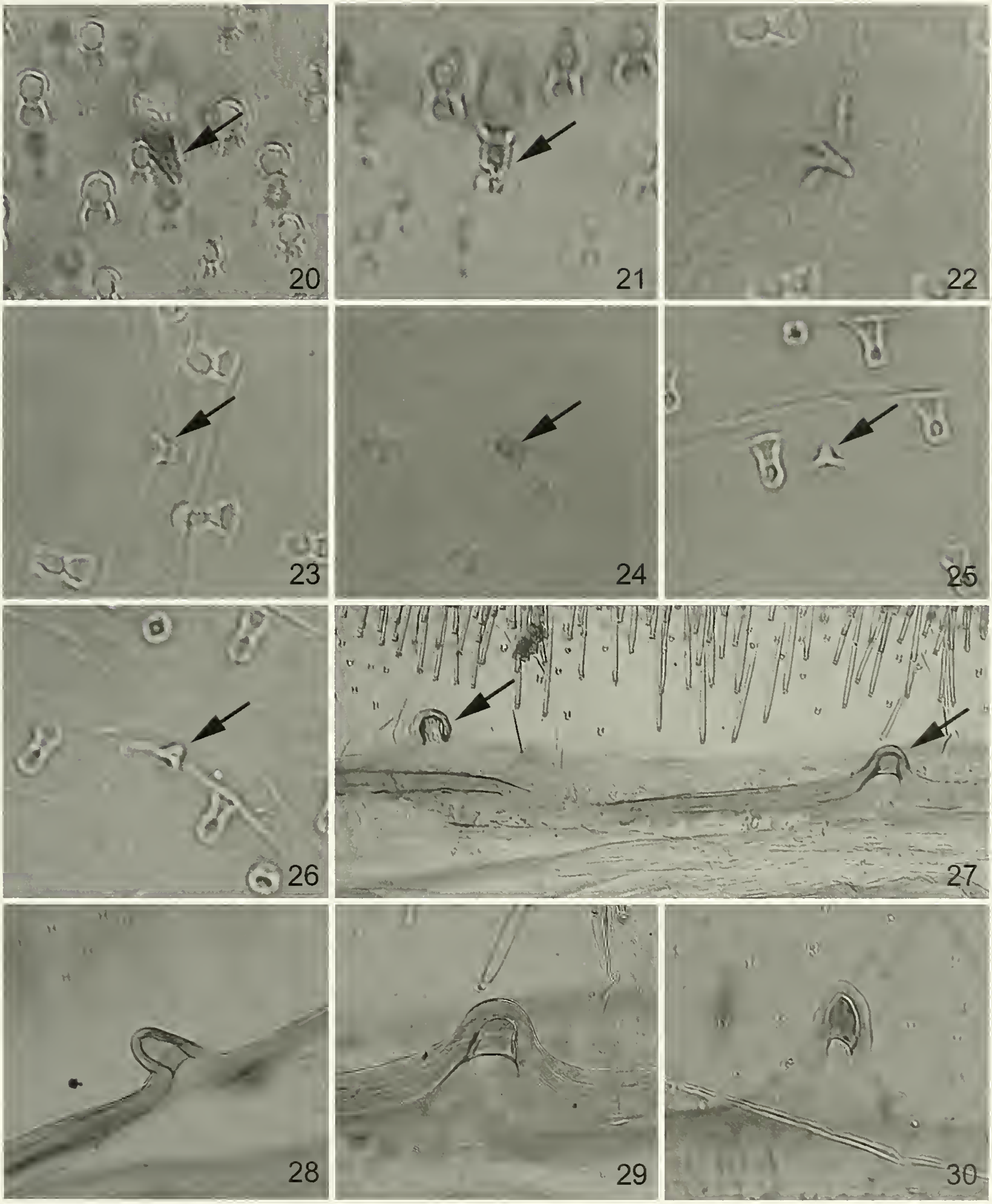
FIG. 1. Abdominal tubercles of *Cossula arpi*.



FIGS. 2-7. Abdominal tubercles. Cossidae, *Cossula arpi*: 2, SEM of interior of tubercle; 3, SEM of tubercle on tergite 7; 4, SEM of tubercles on tergite 7; 5, SEM of tubercle on tergite 7; 6, enlargement of apex of tubercle in 5; 7, enlargement of apex of tubercle in 4.



FIGS. 8-19. Abdominal tubercles. Cossidae, *Cossula arpi*: 8, tubercle on tergite 2; 9, tubercle on tergite 6; 10, tubercle on tergite 8. Dudgeoneidae, *Acritocera negligens*: 11, tubercle on tergite 5; *Dudgeonea* sp: 12, tubercle on tergite 6. Cossidae, *Archaeoses polygrapha*: 13, tubercle on tergite 6. Andesianidae, *Andesiana lamellata*: 14, tubercle on tergite 4; 15, tubercle on tergite 5. Acrolophidae, *Acrolophus popeanella*: 16, tubercle on tergite 4; 17, tubercle on tergite 5. Arrhenophanidae, *Arrhenophanes perspicilla*: 18, tubercle on tergite 2; 19, tubercle on tergite 4.



FIGS. 20-30. Abdominal tubercles. Arrhenophanidae, *Arrhenophanes perspicilla*: 20, tubercle on tergite 4; 21, tubercle on tergite 5. Brachodidae, *Brachodes canonitis*: 22, tubercle on tergite 4; 23, tubercle on tergite 6. Carposinidae, *Carposina nipponensis*: 24, tubercle on tergite 4. Pyralidae, *Condylolomia participalis*: 25, tubercle on tergite 2; 26, tubercle on tergite 5. Megalopygidae, *Megalopyge defoliata*, tuberculate invaginations: 27, tubercles on tergite 4; 28, tubercle on tergite 3; 29, tubercle on tergite 4; 30, tubercle on tergite 5.

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